NeoBiota 69: 155–175 (2021)
doi: 10.3897/neobiota.69.71949
https://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Non-native plant drives the spatial dynamics of its herbivores: the case of black locust (*Robinia pseudoacacia*) in Europe

Richard Mally[1], Samuel F. Ward[2], Jiří Trombik[1], Jaroslaw Buszko[3], Vladimir Medzihorsky[1], Andrew M. Liebhold[1,4]

1 *Czech University of Life Sciences, Faculty of Forestry and Wood Sciences, Kamýcká 129, 165 00 Prague 6 – Suchdol, Czech Republic* **2** *Mississippi State University, Department of Biochemistry, Molecular Biology, Entomology and Plant Pathology, Mississippi State, MS 39762, USA* **3** *Nicolaus Copernicus University, Toruń, Poland* **4** *USDA Forest Service Northern Research Station, 180 Canfield St., Morgantown, WV 26505, USA*

Corresponding author: Richard Mally (mally@fld.czu.cz)

Academic editor: Jianghua Sun | Received 22 July 2021 | Accepted 30 September 2021 | Published 9 November 2021

Citation: Mally R, Ward SF, Trombik J, Buszko J, Medzihorsky V, Liebhold AM (2021) Non-native plant drives the spatial dynamics of its herbivores: the case of black locust (*Robinia pseudoacacia*) in Europe. NeoBiota 69: 155–175. https://doi.org/10.3897/neobiota.69.71949

Abstract

Non-native plants typically benefit from enemy release following their naturalization in non-native habitats. However, over time, herbivorous insects specializing on such plants may invade from the native range and thereby diminish the benefits of enemy release that these plants may experience. In this study, we compare rates of invasion spread across Europe of three North American insect folivores: the Lepidoptera leaf miners *Macrosaccus robiniella* and *Parectopa robiniella*, and the gall midge *Obolodiplosis robiniae*, that specialize on *Robinia pseudoacacia*. This tree species is one of the most widespread non-native trees in Europe. We find that spread rates vary among the three species and that some of this variation can be explained by differences in their life history traits. We also report that geographical variation in spread rates are influenced by distribution of *Robinia pseudoacacia*, human population and temperature, though *Robinia pseudoacacia* occurrence had the greatest influence. The importance of host tree occurrence on invasion speed can be explained by the general importance of hosts on the population growth and spread of invading species.

Keywords

Black locust, Diptera, Lepidoptera, *Macrosaccus robiniella*, *Obolodiplosis robiniae*, *Parectopa robiniella*, *Robinia pseudoacacia*

Copyright *Richard Mally et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Plants introduced to new, non-native habitats may have an advantage over the native flora by escaping herbivore pressure, allowing them to allocate more resources toward vegetative and reproductive growth, as formulated e.g. in the enemy release hypothesis (Keane and Crawley 2002). In such a setting, non-native plants can quickly become widespread and invade various habitats. Black locust, *Robinia pseudoacacia* (Fabaceae), is a prime example of this, now being one of the most widespread non-native trees in Europe (Vítková et al. 2016). The native range of this species is limited to the central Appalachian and Ouachita mountains and the Ozark Plateau in the Eastern and Central United States (Huntley 1990). Black locust was introduced to Europe during the first half of the 17th century as an ornamental tree planted in parks and gardens (Wein 1930), and from 1750 on, it was used in forest plantations in Central Europe for purposes of timber and honey production. From these plantings, it spread prolifically and is currently found throughout most of temperate and sub-Mediterranean Europe (Fig. 1A), displacing native vegetation and altering ecosystem properties (Vítková et al. 2016).

Although widely distributed, European populations of black locust were little affected by the few native generalist herbivores feeding on it, with generally marginal impact on the tree (e.g. Bartha et al. 2008). In contrast, five specialist herbivores accidentally introduced to Europe from the native range of black locust were found to have a considerably higher impact on the tree. The first North American insect species discovered feeding on *Robinia* in Europe was the sawfly *Euura tibialis* (Newman, 1837) (Hymenoptera: Tenthredinidae), formerly placed in *Nematus* (Prous et al. 2014). This species was first recorded in Europe in 1825 (Rasplus et al. 2010), twelve years before the species' formal description from the Isle of Wight (Newman 1837). In Europe, this parthenogenetic species is found feeding on *Robinia pseudoacacia* and *R. viscosa*, while in its original North American range it also feeds on *R. hispida* and *Gleditsia triacanthos* (Darling and Smith 1985; Liston 2011).

More recently, four additional *Robinia* herbivores were accidentally introduced from North America to Europe: In 1970, *Parectopa robiniella* Clemens, 1863, a Lepidoptera leaf miner of the Gracillariidae family, was recorded from Northern Italy (Vidano and Marletto 1972). It was followed by *Appendiseta robiniae* (Gillette, 1907) (Aphididae), an aphid first found in 1978 in Italy (Micieli De Biase and Calambuca 1979). Another Gracillariidae leaf miner, *Macrosaccus robiniella* (Clemens, 1859), was first found in 1983 in Northern Switzerland (Whitebread 1990). This species was placed in *Phyllonorycter* Hübner, 1822 until recently, when it was transferred to *Macrosaccus* Davis & De Prins, 2011 (Davis and De Prins 2011). Finally, in 2003 the black locust gall midge, *Obolodiplosis robiniae* (Haldeman, 1847) (Diptera: Cecidomyiidae), was reported from Northeast Italy (Duso and Skuhravá 2002). Upon the arrival of the four most recently introduced *Robinia* herbivores in Europe, black locust was widely distributed and naturalized on the continent. The four herbivore species thus found their food source in abundance and were subject to little competition from more generalist native European herbivores, so that they could extend their distribution range.

Relatively little is known about how the range expansion of specialized non-native herbivorous insects is affected by the distribution of their native host plant in non-native regions. European *Robinia pseudoacacia* and its introduced specialist herbivores are a prime opportunity to study such a setting in more detail. In order to better understand the factors promoting the range expansion of these non-native herbivores and to better predict spread patterns in other parts of black locust's non-native range, we analyze the three most well-documented *Robinia* herbivores present in Europe (*P. robiniella*, *M. robiniella*, and *O. robiniae*), their patterns of historical spread across the continent, and potential factors facilitating this spread. For this, we investigate and quantify different potential drivers of the spread of these herbivores: *Robinia* distribution, human population, mean annual temperature and precipitation, and proximity to previously invaded regions. We hypothesize that both the human population and *R. pseudoacacia* distribution would positively affect herbivore spread via effects on propagule pressure and habitat invasibility.

Methods

In order to avoid confusion among the similar species names, we will refer to the three species by their genus names, i.e., *Parectopa* for *P. robiniella*, *Macrosaccus* for *M. robiniella*, and *Obolodiplosis* for *O. robiniae*. In figures and tables, we state the full species names. We furthermore refer to *Robinia pseudoacacia* simply as *Robinia*, unless other *Robinia* species are mentioned.

Country and regional first records of the presence of *Parectopa*, *Macrosaccus* and *Obolodiplosis* across Europe were obtained from the published literature, online databases and in one case from a photographic record. Coordinates for the localities were obtained through Wikipedia's GeoHack (https://www.mediawiki.org/wiki/GeoHack) and Google Maps (https://www.google.com/maps). Suppl. material 1: Table S1 provides a full list of records for the three folivore species. We also obtained georeferenced occurrence records for each of these three species at a global scale. These were sourced from GBIF (https://www.gbif.org), EPPO (https://gd.eppo.int), CABI (https://www.cabi.org/ISC), Davis and De Prins (2011) and Shang et al. (2015). These global records were not used for analysis of spread rates.

Radial rates of spread were estimated for each species from European first records using the distance regression method (Gilbert and Liebhold 2010). According to this method, a linear regression model was fit to the distance from the first discovery point in Europe as a function of year of first discovery. The slope of the estimated regression equation provides an estimate of the radial rate of range expansion. Distances between the distribution records were calculated with the R packages geosphere 1.5-10 (Hijmans et al. 2019) and sp 1.4-2 (Pebesma and Bivand 2005; Bivand et al. 2013), using the 'Vincenty' (ellipsoid) great circle distance function (distVincentyEllipsoid). Linear regressions were performed using the *lm* function in the R language.

In order to explore factors affecting spread of each species, we applied Cox Proportional Hazard analysis following the approach used by Ward et al. (2020). This model quantifies the probability that each uninvaded location will become invaded at annual time steps as a function of a series of candidate explanatory variables. Five predictors for herbivore spread were considered: human population, *Robinia* distribution, mean annual precipitation, mean annual temperature (see Fig. 1), and spatial proximity. Human population (expressed as number of inhabitants in the year 2000) was extracted from a human population density raster at a resolution of 30 arc-seconds from the Global Rural-Urban Mapping Project (Balk et al. 2006). Data on *Robinia* distribution (expressed as total tree area in km^2) were extracted from the European Atlas of Forest Tree Species (Sitzia et al. 2016) as a relative probability of presence raster at a resolution of 1 km, based on the C-SMFA model and field observations (de Rigo et al. 2016). Values of total annual precipitation (cm) and annual mean temperature (°C) for the period 1970–2000 were obtained from the WorldClim v2 database (Fick and Hijmans 2017) at a resolution of 30 arc-seconds. No data on *Robinia* distribution were available for points located in Moldova, Belarus, Ukraine and the European part of Russia. Values for each variable were calculated for areas in a 10 or 50 km buffer radius zones around each of the individual records for each species. Spatial proximity (*sp*) to previously invaded points (associated with diffusive propagule pressure) was a time-varying predictor and calculated as:

$$\text{spatial proximity } sp = \sum_{i=1}^{n} \frac{1}{d_{ij}},$$

where d is the distance (in km) between a given point i and each previously invaded point j. Thus, spatial proximity was estimated for each point in each year, while all other predictors did not change annually. Human population and *Robinia* distribution were log-transformed to reduce skewness.

In addition to locations of individual records for each species, the Cox proportional hazard model was fit using "pseudo-absence" points. These are locations falling outside of the invaded range of each species that were never invaded during the time span of records. Pseudo-absence records were generated in a 50 km grid across a 300 km buffer zone outside of the minimum convex hulls around each set of records for each species (see Fig. 2). The minimum convex hull, individual buffer zones and spatial statistics for the selected variables were created using ESRI ArcMap 10.5.1 (ESRI 2016).

Given uncertainty about the identity of most relevant spatial scales of the predictor variables, all possible combinations of 10 km and 50 km scale predictors were fit in full models. The model with the lowest Akaike Information Criterion (AIC; Akaike 1973) was then further reduced (if applicable) by iteratively removing predictors with the higher p-value until all remaining were $p < 0.05$. To assess robustness of our models to the missing values of *Robinia* density for Eastern Europe, the entire model fitting and selection process was redone without considering *Robinia* distribution as a predictor. Models were fit using the R package survival 3.2-7 (Therneau 2020).

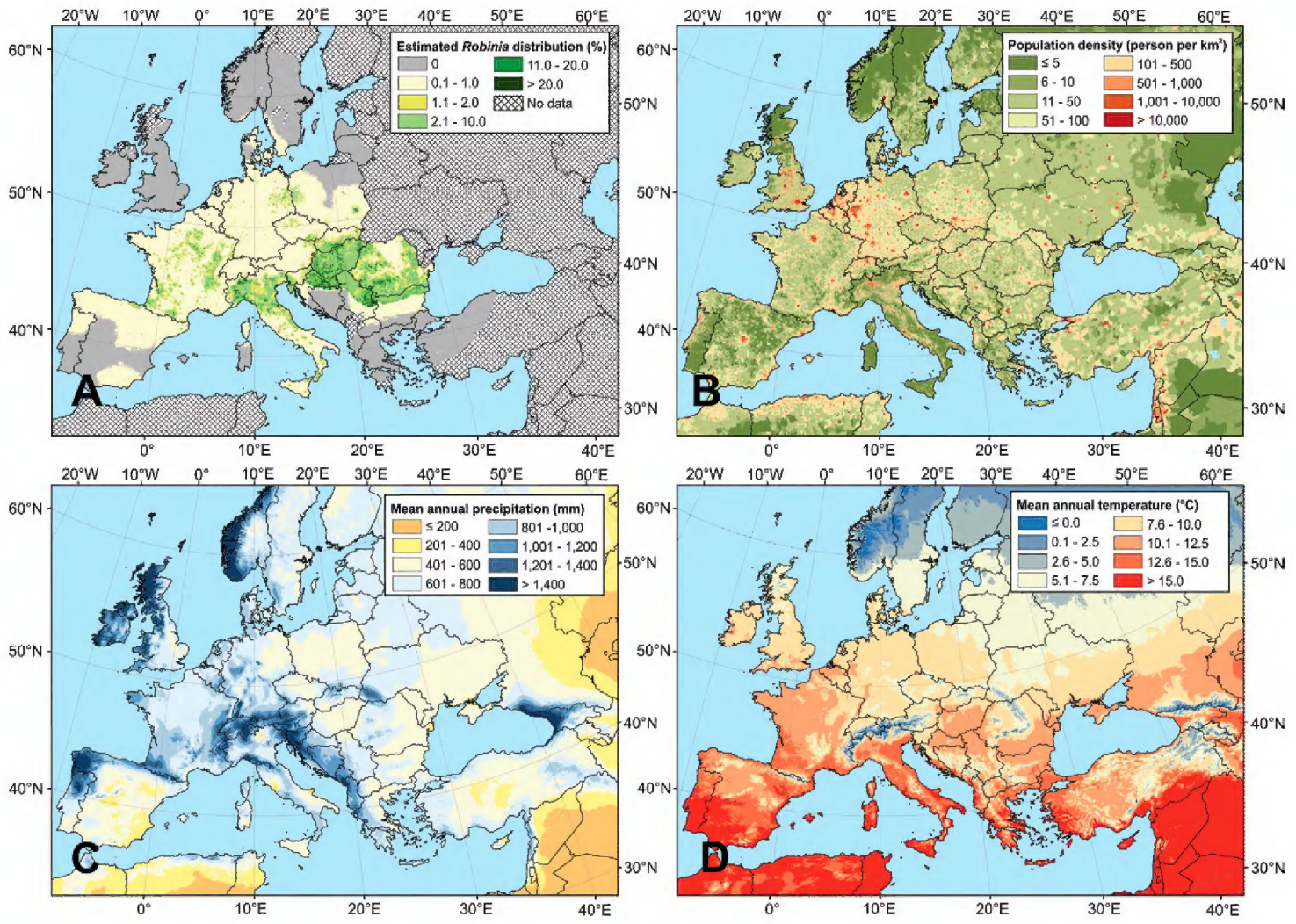

Figure 1. Variables investigated for their influence on the spread of the three *Robinia*-specific herbivores in Europe **A** estimated distribution of *Robinia pseudoacacia* **B** human population **C** mean annual precipitation **D** mean annual temperature.

Results

We assembled 97 first record locations from 24 countries for *Parectopa*, 92 locations from 25 countries for *Macrosaccus*, and 75 locations from 33 countries for *Obolodiplosis* (Fig. 2; Suppl. material 1: Table S1; Mally et al. 2021). Linear regressions show a highly significant correlation between time and distance from the invasion focus for all three herbivores: the radial rate of spread estimated by linear regression (Fig. 3) is 35.4 ± 5.7 km/year (t_{95} = 6.16, p < 0.005) for *Parectopa*, 73.42 ± 5.0 km/year (t_{90} = 14.79, p < 0.005) for *Macrosaccus*, and 128.3 ± 8.1 km/year (t_{73} = 15.79, p < 0.005) for *Obolodiplosis*.

Macrosaccus mainly spread east- and northward in the first two decades after its introduction (Fig. 2B), as did *Parectopa*. The latter species was first discovered in Northern Italy, south of the Alps. In order to reach the areas north of the Alps, it spread east- and later northward around this mountain range that acted as a geographical barrier (Fig. 2A). *Obolodiplosis* spread more or less equally in all directions from its first occurrence location in Northern Italy. Within Europe, it is the most widespread of the three investigated *Robinia* herbivores, with distribution records stretching from Portugal to the Caspian Sea and from Sicily to Southern Sweden and the Baltic states

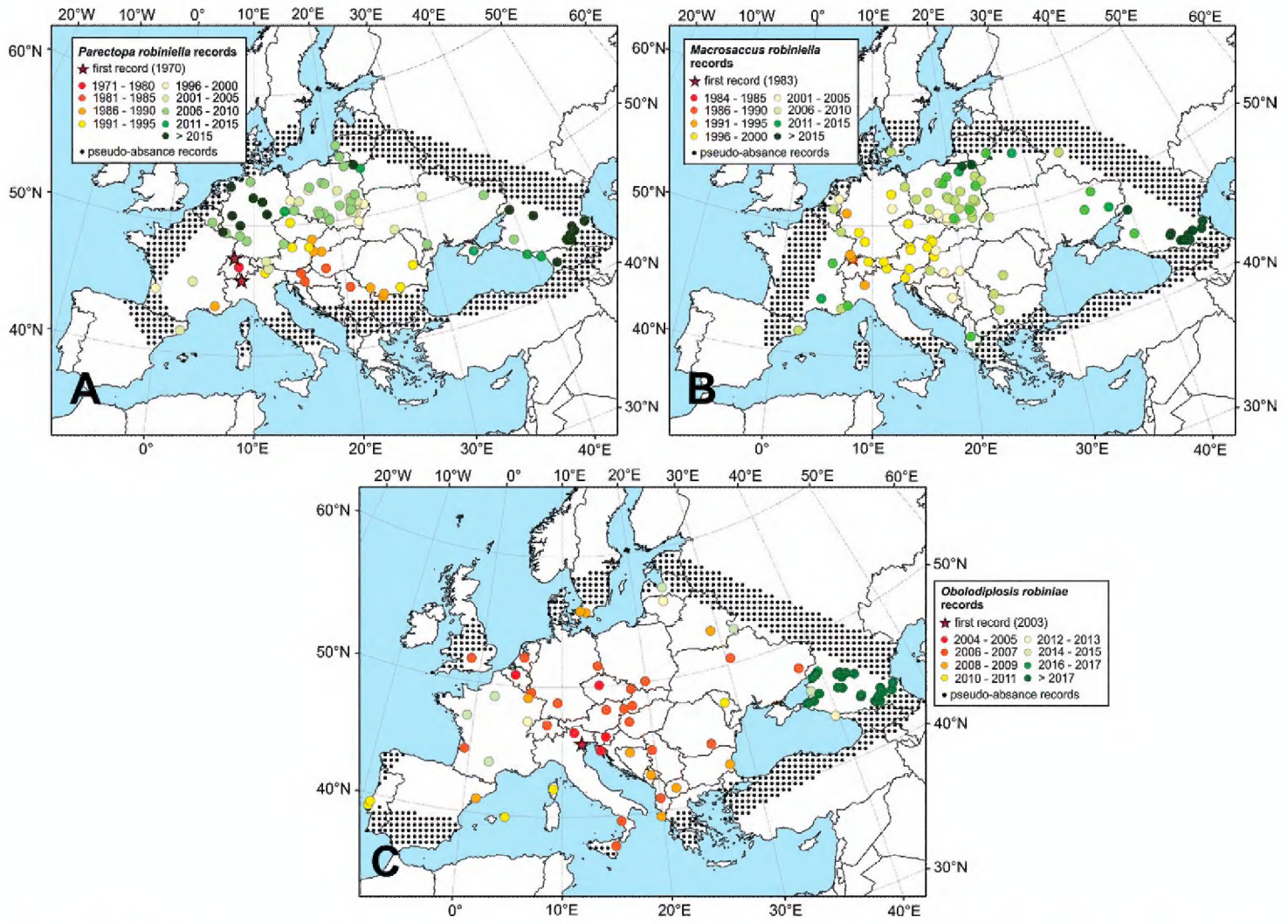

Figure 2. European records for **A** *Parectopa robiniella* **B** *Macrosaccus robiniella*, and **C** *Obolodiplosis robiniae*. The first European record for each species is marked by a star, the subsequent spread is indicated by color-coded records in 5-year (**A, B**) or 2-year (**C**) intervals. The grid of black points around the distribution areas marks pseudo-absence locations in a 300 km buffer region formed by the minimum convex hull around the records for each species.

(Fig. 2C). In the 18 years since its first discovery in Europe, it has invaded a larger area than either of the two leaf miners, which had been introduced considerably earlier.

Results of the reduced Cox proportional hazard models are shown in Table 2, correlation matrices of predictors for the best-fitting model for the three species in Suppl. material 2: Tables S4–S6, and Akaike Information Criterion (AIC) values for the three species in Suppl. material 2: Tables S7–S9. Annual mean precipitation is found to have the least predictive power among the five investigated predictors. It is absent in all reduced models (Table 2), and is significant only for *Parectopa* in the full model (Suppl. material 2: Table S2). In the reduced (Table 2) and full (Suppl. material 2: Table S2) models, colder annual mean temperatures were associated with an increased risk of invasion for *Parectopa* and *Macrosaccus* (as indicated by the negative Z-scores), and less so for *Obolodiplosis*. In the models with *Robinia* omitted (Suppl. material 2: Table S3), it is significant for *Parectopa*, and less so for *Macrosaccus*; no significance is observed for *Obolodiplosis*. In the full and the reduced models, human population has a highly significant positive influence on the invasion risk for *Parectopa* and *Macrosaccus*, and less so for *Obolodiplosis*. In the models with *Robinia* omitted (Suppl. material 2: Table S3), it is highly significant for all three species. *Robinia* distribution is found to be the most

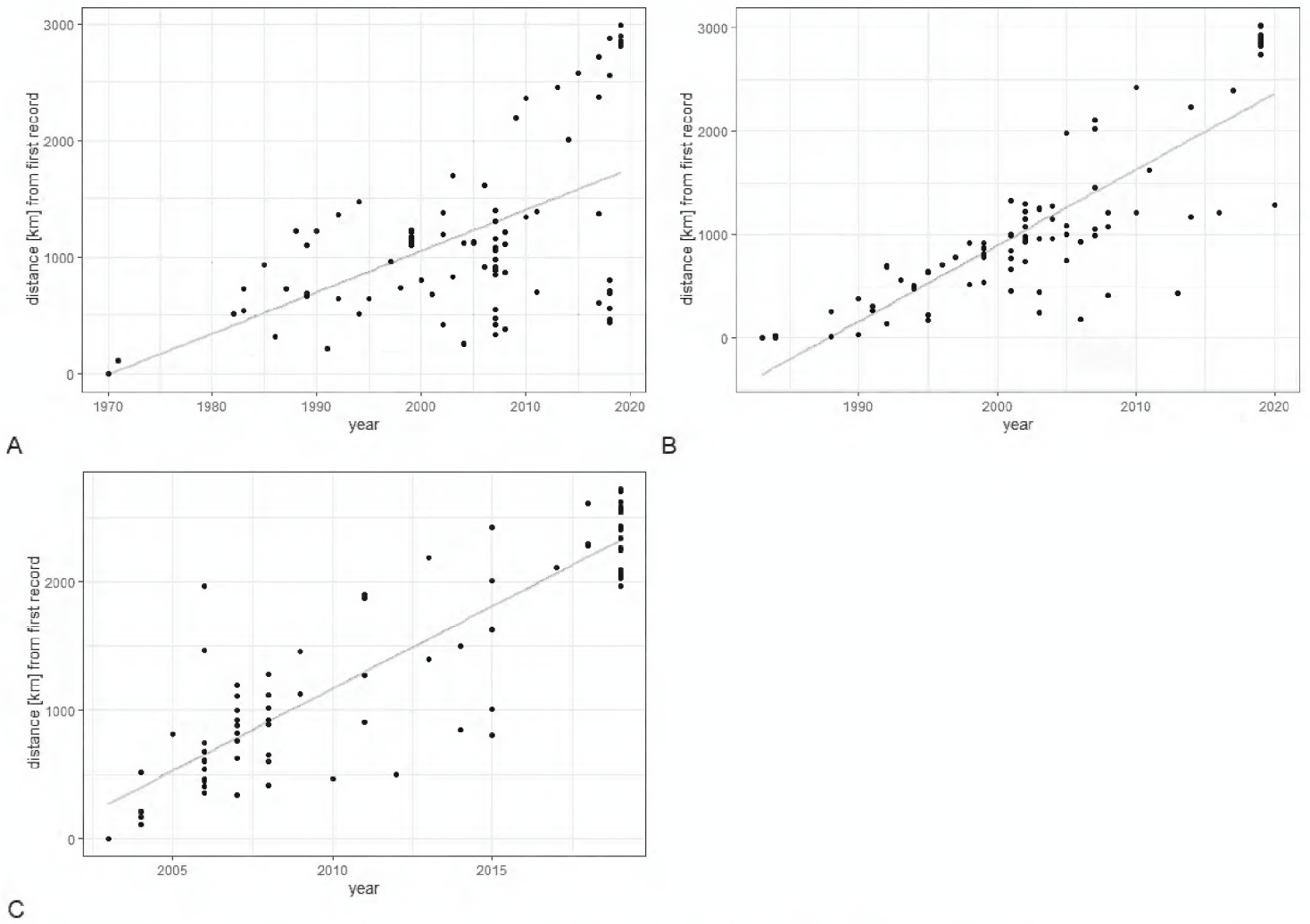

Figure 3. Linear regression scatterplots of distance (in km) from first record in Europe over time, for **A** *Parectopa robiniella* **B** *Macrosaccus robiniella*, and **C** *Obolodiplosis robiniae*.

Table 1. Results of the linear regression of distance over time for the three herbivore species. Radial rate of spread (km per year) is provided by the slope of the regression.

	Intercept ± SE	Slope (radial rate of spread) ± SE	Multiple R-squared
Parectopa robiniella	-10.06 ± 201.60	35.37 ± 5.7	0.29
Macrosaccus robiniella	-354.72 ± 107.55	73.42 ± 5.0	0.71
Obolodiplosis robiniae	270.69 ± 84.08	128.29 ± 8.12	0.77

Table 2. Results of reduced Cox proportional hazards (CPH) models with lowest AIC and all predictors with $p < 0.05$.

Species	Predictor	Coefficient	SE	*Z*	*p*
Parectopa robiniella	spatial proximity *sp*	3.67	0.80	4.59	<0.0001
	human population (50 km)	0.61	0.09	6.61	<0.0001
	Robinia (10 km)	0.59	0.07	7.89	<0.0001
	temperature (50 km)	-0.61	0.08	-8.10	<0.0001
	precipitation (10 km)	-0.0032	0.0011	-2.98	0.0029
Macrosaccus robiniella	spatial proximity *sp*	22.87	2.61	8.78	<0.0001
	human population (10 km)	0.58	0.08	7.64	<0.0001
	Robinia (50 km)	0.40	0.06	6.76	<0.0001
	temperature (50 km)	-0.58	0.09	-6.37	<0.0001
Obolodiplosis robiniae	spatial proximity *sp*	40.08	15.74	2.55	0.0109
	human population (10 km)	0.37	0.11	3.35	0.0008
	Robinia (50 km)	0.44	0.06	7.05	< 0.0001
	temperature (50 km)	-0.13	0.06	-2.07	0.0382

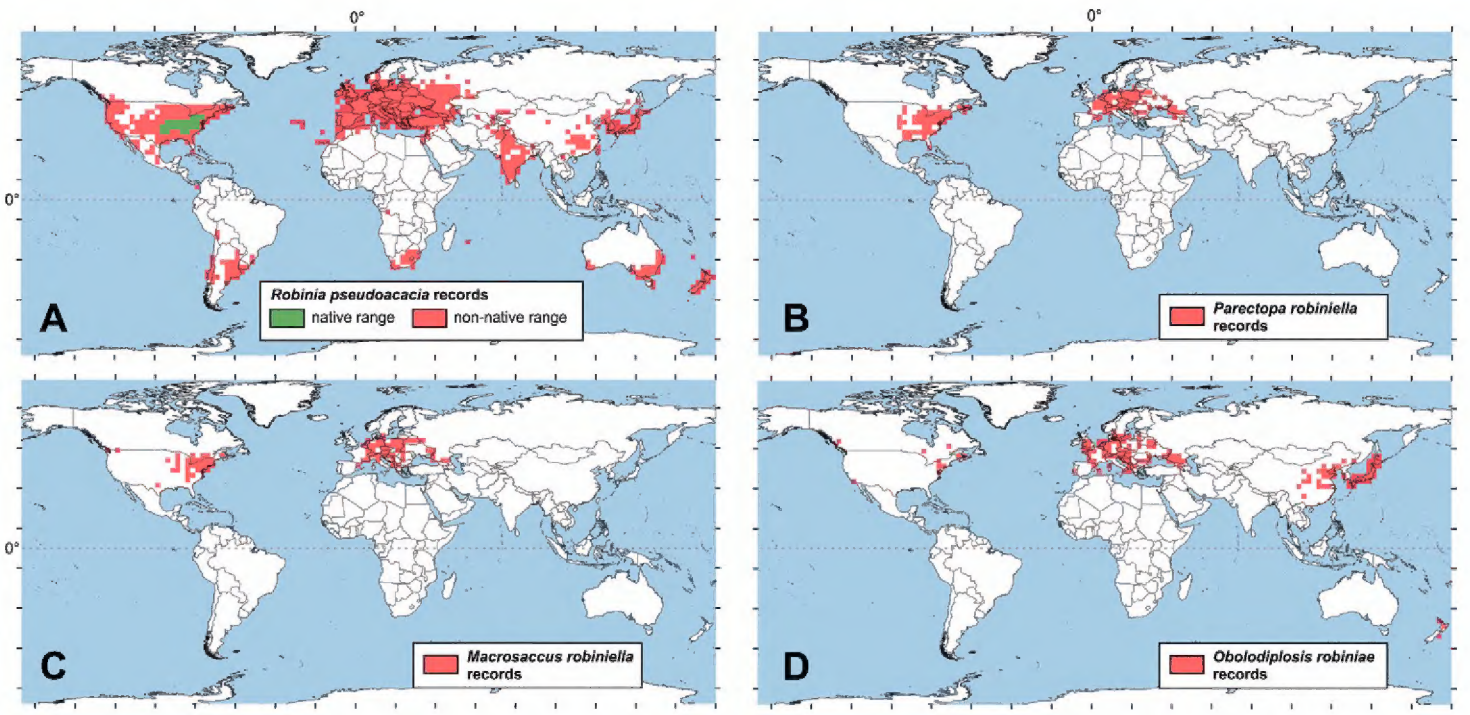

Figure 4. Global distribution of **A** *Robinia pseudoacacia* **B** *Parectopa robiniella* **C** *Macrosaccus robiniella* and **D** *Obolodiplosis robiniae* compiled from our own dataset, GBIF, EPPO, CABI, Davis and De Prins (2011) and Shang et al. (2015).

consistent predictor, explaining the spread of all three species with high significance both in the full and the reduced models. In the full and the reduced models, proximity to previously invaded areas is highly significant for *Parectopa* and *Macrosaccus*, but much less so for *Obolodiplosis*. In the models without *Robinia*, it is highly significant for all three species, along with human population.

The known global distribution of *Robinia* is shown in Fig. 4A, and the distributions of the three herbivore species are shown in Fig. 4B–D. *Robinia* is widely distributed in virtually every temperate and subtropical portion of the world. The distributions of the three herbivore species appear to be more limited. Of the three species, *Obolodiplosis* is the most widely distributed, having established in Europe, East Asia and New Zealand. However, there is no record of its presence in either the Afrotropic or Neotropic regions. The two Lepidoptera species *Parectopa* and *Macrosaccus* appear to be slightly less successful invaders, having only established in Europe.

Discussion

The three herbivores show similar patterns of radial range expansion in Europe, although with substantially different annual spread rates. All three species were initially discovered in the same general region of south-central Europe with only ~200–400 km separating their sites of initial discovery. Strikingly, *Parectopa*, which was the first of the three investigated *Robinia* herbivores to be recorded from Europe over 50 years ago, has the smallest annual spread rate (about 35 km/year) and is reported from the fewest number of countries (24). *Macrosaccus*, first reported 13 years later in 1983, exhibits an average spread rate of 73 km/year, but spread much faster in Hungary with

its abundant black locust stands, invading the entire country from west to east in two years (Csóka 2001). The species is currently recorded from 25 European countries. The newest invader, *Obolodiplosis*, has the by far highest spread rate (128 km/year) and has spread to 33 countries since its first report in 2003. Of the three species, *Obolodiplosis* has also spread the most widely on the global scale (Fig. 4D). While *Obolodiplosis* has successfully invaded Europe, East Asia and New Zealand, *Parectopa* and *Macrosaccus* have only invaded Europe. In North America, all three species have also extended their range beyond the native range of *Robinia*, with *Macrosaccus* and *Obolodiplosis* having spread as far as the west coast of the US and Canada.

Invasion spread is driven by population growth coupled with movement. Thus, any factors that affect either population growth or movement are likely to influence patterns of spread. It is likely that the differences in invasion patterns observed among these species (both within Europe and globally) can be attributed to their biological traits that influence their population growth rates or dispersal, either natural dispersal or accidental long-distance movement by humans. *Obolodiplosis* develops through three generations per year in the Czech Republic, and in up to four generations in more southern regions such as Italy, Hungary and Serbia (Skuhravá et al. 2007; Mihajlović et al. 2008; Duso et al. 2011). For China, however, up to six generations per year have been reported (Shang et al. 2015). The capacity for this species to develop through multiple generations likely facilitates rapid population growth (Fahrner and Aukema 2018). The small size of adults also probably leads to this species being easily transported in wind though such natural dispersal probably only facilitates local dispersal. Long-distance transport (including inter-continental spread) is most likely to occur via hitch-hiking with cargo, vehicles, etc. Pupation of *Obolodiplosis* takes place in the galls, except for the last generation of a year, where pupation takes place in the soil (Uechi et al. 2005; Tóth et al. 2009). Because this species overwinters as a diapausing larva (Duso et al. 2011), this probably creates potential for the species to be accidentally transported long distances with vehicles and other objects that might be placed under *Robinia* trees prior to transport.

Even though both of the two leaf miner species belong to the same Lepidoptera family (Gracillariidae), their biologies exhibit differences that potentially explain differences observed in their success and rate of spreading across Europe. *Parectopa* produces two to three generations per year, with two in more northern regions such as Belarus, and up to three in more southern regions like Transnistria (Moldova) and Croatia (Maceljski and Igrc 1984; Antyukhova 2010; Sautkin and Evdoshenko 2012). *Macrosaccus* is reported to produce two to five generations per year: two generations in Southern Germany, Switzerland and Austria (Wipking 1991; Huemer et al. 1992; Huemer 1993; Rietschel 1996), two to three generations in Hungary (Csóka 2001), three generations in Serbia and Belarus (Stojanović and Marković 2005; Sautkin and Evdoshenko 2012), four generations in Slovenia (Seljak 1995), and potentially even a fifth generation in Croatia (Maceljski and Mešić 2001). Furthermore, often two to three (and up to eight) *Macrosaccus* larvae share a common mine (Huemer 1993; Rietschel 1996; Šefrová 2001), whereas *Parectopa* caterpillars usually inhabit

mines solitarily (Baugnée 2014). In addition to a generally higher reproduction rate, *Macrosaccus* may thus be able to attain a higher population density.

Pupation takes place in the leaf litter in the case of *Parectopa*, whereas *Macrosaccus* larvae pupate on the leaves (Antyukhova 2010; Davis and De Prins 2011). In urban areas, *Parectopa* pupae might therefore be removed with the leaf litter in the autumn (Antyukhova 2010), whereas *Macrosaccus*, which overwinters in the adult stage (Deschka 1995), probably remains on or near its host plants, increasing its chances of re-occupying *Robinia* stands in the following season. However, pupating in the leaf litter, where it is presumably less exposed to parasitoids, might increase the survival of *Parectopa* as compared to *Macrosaccus* (Csóka et al. 2009). Given that *Parectopa* exhibits the slowest rate of spread of all three species, we can hypothesize that their biology of overwintering as pupae in leaf litter does not facilitate their anthropogenic movement to the extent seen in *Macrosaccus* and *Obolodiplosis*.

The small adult body size and wing anatomy of the two leaf miners indicate that they likely spread passively with wind, but transport of hibernating or resting adults with trade cannot be excluded (Rietschel 1996; Šefrová 2001, 2003). Passive wind transportation might explain the generally stronger eastward spread of the leaf miners with the prevailing west winds in Central Europe.

We find a negative correlation between mean annual temperature and the spread of the two leaf miners, meaning that colder temperatures promote the spread of these species. Considering the geographical setting in which the range expansion of these species occurred, this is not surprising: with their first records in Northern Italy resp. Northern Switzerland, range expansion would occur mostly north- and eastward, as expansion southwards is limited by the Mediterranean Sea. The negative correlation between temperature and spread might thus be a result of generally more sampling points in the north- and eastward direction of the points of first record, where annual mean temperatures are generally lower than those in Northern Italy (see Fig. 1D).

Our findings of colder annual mean temperatures promoting the spread of both leaf miners are in contrast to published information at least of *Parectopa*, which is reported to be "more thermophilous" than *Macrosaccus* (Baugnée 2014). This is consistent with its slower northward spread and its presence in Southern Italy (i.e., south of the Emilia Romagna region), where *Macrosaccus* is absent (Stoch 2003). *Parectopa* was also reported as "massively present" with 50–80% of leaflets infested in the hot and dry, sandy environments of coastal Croatia, whereas habitats in inland Croatia with a more continental climate experienced a low infestation rate of 3% (Maceljski and Igrc 1984; Stojanović and Marković 2005). *Parectopa* thus seems to have more specialized habitat requirements than *Macrosaccus*. *Parectopa* might therefore continue its spread in the more southern parts of Europe and into the Transcaucasian region where its hostplant is present. Fodor and Hâruța (2009) find almost no niche overlap between *Parectopa* and *Macrosaccus* in Romania, despite both utilizing *Robinia* leaves as their food source, where they occupy mostly opposite sides and different parts of the leaflets. The two leaf miners are thus not in direct competition for their food source.

Both leaf miner species are often reported to exhibit high population densities during their initial colonization phase following establishment in a new region, while subsequently becoming much rarer (Seljak 1995; Šefrová 2001; Tomov 2003; Antyukhova 2010; Baugnée 2014). In Poland however, *Parectopa* was mostly first recorded from single mines in isolated locations, apparently as a result of anemochorous dispersal. The following absence of *Parectopa* mines in these locations for several years suggests that these founder populations were unable to establish. More successful northward spread of *Parectopa* occurred along river valleys, e.g. the Vistula valley, where *Robinia* finds favorable growing conditions on the sunny slopes (JB, pers. obs.). *Macrosaccus*, on the other hand, quickly spread through Poland over a wide front and in considerable abundance until 2005, when areas of rarer *Robinia* occurrence (presumably due to less suitable growth conditions) were reached (JB, pers. obs.). There are also records of *Obolodiplosis* being very abundant in recently invaded regions, particularly in East Asia (Yang et al. 2006). Though lacking quantitative data, it appears that none of the three species is particularly abundant in their native range in North America (AML, pers. obs.). Along these lines, we note that most of the records of *Obolodiplosis* from North America lie outside of the native range of its host, *Robinia*, which may be indicative of the low abundance of *Obolodiplosis* in its native range.

Parasitization might play an important role in the speed of spread. Since their establishment in Europe, the two leaf miners have accumulated a large number of generalist parasitoids (summarized in Serini 1990; De Prins and De Prins 2006–2020, and Csóka et al. 2009), with 20 species recorded for *Parectopa*, and 37 for *Macrosaccus*. Parasitization rates vary considerably though, ranging in the case of *Macrosaccus* from 1–3% in Upper Austria (Deschka 1995), 10–30% in Southern Moravia (Šefrová 2001), <40% in Kraków, Poland (Wojciechowicz-Żytko and Jankowska 2004), 35–50% in Trentino, Italy (Angeli et al. 1996), up to 47.6% in Hungary (Csóka et al. 2009), and >60% in Bosnia-Herzegovina (Dimić et al. 2000), to 30–67.5% in Serbia (Stojanović and Marković 2005). Information on parasitization rates in *Parectopa* are few, reaching a maximum of 15.3% in Hungary, where *Macrosaccus* is up to three times more heavily parasitized (Csóka et al. 2009). *Obolodiplosis* hosts few parasitoids, which likely promotes its rapid spread in Europe and other regions of the world. It is to be expected that *Obolodiplosis* will have a fairly large impact on *Robinia* populations wherever it is introduced, which might however be compensated by the fast growth and reproductive abilities of *Robinia*. On the other hand, *Platygaster robiniae*, the gall midge's primary parasitoid infesting the host eggs and feeding gregariously on the larvae (Buhl and Duso 2008; Duso et al. 2011; Kim et al. 2011), is reported to cause parasitization rates of 51.6% to 84.8% (Park et al. 2009; Lu et al. 2010), making it a promising candidate as control agent of the locust gall midge (Lu et al. 2010).

Our quantitative analysis indicates local *Robinia* density to be the single factor having the strongest impact on the spread of *Parectopa*, *Macrosaccus* and *Obolodiplosis* across Europe. Skuhravá et al. (2007) reached a similar conclusion for *Obolodiplosis* based on a qualitative evaluation of historical European spread. Since feeding of all three insect species is limited to *Robinia*, it is understandable that its density would

strongly affect population growth rates and consequently affect spread. Several other studies have reported that host densities influence rates of invasion spread of invading species (e.g., Meier et al. 2014; Hudgins et al. 2017; Ward et al. 2020). The resource concentration hypothesis posits that more abundant host plant resources promote insect herbivore population growth rates (Hambäck and Englund 2005), and such elevated rates can be expected to translate into increased invasion spread rates.

The fact that *Robinia* is itself an invasive species has interesting implications regarding the positive effect of *Robinia* density on spread of these folivore species. It has been noted that at a global scale, plant invasions or widespread planting of non-native plants promote invasions by herbivore species that use these plants as hosts (Liebhold et al. 2018; Branco et al. 2019; Guo et al. 2019). There are many examples in which abundant distributions of non-native plants have promoted invasions by insect herbivores that specialize on those plants (e.g., Hurley et al. 2016). This phenomenon can be regarded as a type of "invasion meltdown" where invasion by one species triggers subsequent invasions of other species (Simberloff and Von Holle 1999). However, less is known about how host insect invasions can mediate invasions of their parasites beyond theoretical studies (e.g., Fagan et al. 2002).

Previous studies have also identified human population density to be related to the spread of invading insect species (Gilbert et al. 2004; Ward et al. 2020). It is logical that humans may accidentally transport insect life stages and therefore promote long-distance dispersal. Population models show that when occasional long-distance dispersal is coupled with frequent short-distance dispersal, this leads to much greater rates of spread than when long-distance spread is lacking (Shigesada et al. 1995; Hastings et al. 2005). Long-distance dispersal is often associated with passive movement by humans and thus high human densities may drive higher rates of long-distance movement and thereby facilitate invasion spread (Gippet et al. 2019). But the significant influence of human population may also be confounded with *Robinia* occurrence since human-caused disturbance typically promotes this tree species (Vítková et al. 2016).

Similar to human population, annual mean temperature was found to have a significant influence on the spread of the two leaf miners, but less so for the gall midge. This result is in concordance with the wider climate spectrum of invaded regions of *Obolodiplosis*: in Europe, the gall midge is now distributed from the hot-summer Mediterranean climate of Portugal, Sicily and Greece to the humid continental climate of Southern Sweden and the Baltic states. On the global scale, it has been recorded from Vancouver Island, Canada (Skuhravá et al. 2007), Japan and South Korea (Kodoi et al. 2003; Woo et al. 2003; Uechi et al. 2005; Tokuda et al. 2019), China (Yang et al. 2006; Shang et al. 2015), the Russian Far East (Csóka et al. 2017), and New Zealand (Anonymous 2009; Bain 2009) (Fig. 4D). *Parectopa* and *Macrosaccus*, on the other hand, have only been reported outside their native range from Europe and the west coast of North America (Fig. 4B, C). In contrast to mean temperature, we found annual mean precipitation to have no significant influence on the spread of the three herbivore species.

Our results indicate that spatial proximity to previously invaded regions plays an important role for the spread of *Parectopa* and *Macrosaccus*, but much less so for the gall midge *Obolodiplosis*. *Obolodiplosis* showed an extremely fast spread across most of Europe in the 18 years since its first record in Europe, now occupying a considerably larger area than the much earlier established leaf miners. The results of Roques et al. (2016) indicate that it spread faster than any other insect species invading Europe in their analysis. The spread of this species exhibited several long-distance jumps to form discontinuous populations, the most prominent one being a 2,000 km dispersal from its first record in Northeast Italy to the East Ukraine in just three years. Furthermore, *Obolodiplosis* successfully invaded the islands of Great Britain, Sicily, Corfu, and the Balearic Islands, none of which have been reached by either of the two leaf miners. Skuhravá et al. (2007) speculate that the gall midge may frequently be transported over long distances with nursery trees, and/or through passive transport by freight traffic. Our finding that spatial proximity to previously invaded areas plays a minor role in the spread of *Obolodiplosis* concord with its high spread rate of 128.3 km/year, and the observed long-distance dispersal.

None of the scatterplots of the three herbivore species (Fig. 3) show a clear establishment phase preceding the expansion phase. *Macrosaccus*, however, was closely monitored in the area of its first discovery in 1983 around Basel in Northern Switzerland. There, the distribution range did not exceed an 85 km radius around Basel by 1989, although the species was "already common around Basle in 1983" (Whitebread 1990). The absence of a clear establishment phase in the scatterplots might indicate that the species arrived some years before their first record in Europe, when they had time to establish a sufficiently large population and propagule pressure to expand their ranges. The scatterplots also provide little evidence of geographical "saturation" in any of these three species. As invading species spread to all suitable areas in a region, such plots can be expected to asymptotically stop increasing (Shigesada and Kawasaki 1997). Eventually, all three species can be anticipated to become established in all regions with suitable habitat. That environmental niche is presumably defined both by the presence of a suitable climate and by the presence of *Robinia* hosts. Comparison of the current distribution of these species (Fig. 2) with the distribution of *Robinia* suggests that all three species will soon saturate their potential habitat. However, on a global scale these same species are far from saturation and further invasions can be anticipated in the future.

In addition to these three species that utilize *Robinia* as a host, Hargrove (1986) identified 72 other herbivore species associated with *Robinia* in its native North American range. Given the three species studied here, along with *Euura tibialis* and *Appendiseta robiniae*, it is evident that only five out of 75 North American *Robinia* specialists have presently invaded Europe. Thus, we can anticipate that additional herbivore species are likely to invade Europe and elsewhere in *Robinia*'s invaded range and that this will contribute to the dilution of enemy release in populations of this invasive plant.

Conclusion

Specialist herbivores are crucially dependent on the presence of their host plant. Our results show that the widespread presence of *Robinia* in Europe, especially in human-influenced environments, greatly facilitated the spread of the introduced North American herbivores. The excessive proliferation of *Robinia* increases the likelihood of establishment and spread of non-native specialist herbivores, thus creating a negative feedback where the initial beneficial effects of enemy release on *Robinia* are diminished, and *Robinia* populations are potentially reduced.

With *Robinia* having been introduced to most regions of the world with a suitable temperate climate, conditions are thus beneficial for the establishment of these insects, and potentially other specialist herbivores from black locust's native range. *Obolodiplosis* has already become established in East Asia and New Zealand, where it has exhibited rapid spread similar to that in Europe. Its success can be attributed to the ability for long-distance jumps as well as to life history traits, such as high reproduction rates, and a presumably small guild of parasitoids. For the two leaf miner species, spatial proximity to previously invaded areas is another important factor affecting range expansion, reflecting the ability of these species to disperse into adjacent uninvaded areas following initial colonization. Although the three investigated herbivores invaded Europe under similar conditions, there are pronounced differences in their invasion success, which can be explained with species-specific life history traits. Furthermore, pan-European cargo traffic has increased over the past decades, increasing the likelihood of long-distance spreading.

Acknowledgements

We are grateful to Lenka Pešková (ČZU library), Josep Ylla (Gurb (Barcelona), Spain), Elisenda Olivella (Natural Sciences Museum of Barcelona, Spain), Ivan Bacherikov (Saint Petersburg State Forest Technical University, Russia), Jan Havlíček (Karolinum Press, Charles University Prague, Czech Republic), Valentyna Meshkova (Ukrainian Research Institute of Forestry and Forest Melioration, Kharkiv, Ukraine) and Hana Šefrová (Mendel University Brno, Czech Republic) for help with literature search and acquisition. Nico Schneider (Ministère de l'Education nationale, Luxembourg), Erik van Nieukerken (Naturalis Leiden, the Netherlands), Vladimir Krpach (State University of Tetova, North Macedonia), Charles Eiseman (Northfield, Massachusetts, USA) and Francesca Vegliante (Museum für Tierkunde Dresden, Germany) helped with information on distribution records.

This research was supported by the grant "Advanced research supporting the forestry and wood-processing sector's adaptation to global change and the 4th industrial revolution," No. CZ.02.1.01/0.0/0.0/16_019/0000803 financed by OP RDE, as well as by the IGA A_21_21 project of the Czech University of Life Sciences internal grant agency.

The authors declare that there is no conflict of interest regarding the publication of this paper.

References

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csáki F (Eds) 2nd International Symposium on Information Theory, Tsahkadsor, Armenia, USSR, September 2–8, 1971, Budapest: Akadémiai Kiadó, 267–281.

Angeli G, Apollonio N, Forti D (1996) Behaviour of leaf miner *Phyllonorycter robiniellus* (Lepidoptera Gracillariidae) in Trentino surroundings and possibility of control. Informatore Fitopatologico 10: 50–54.

Anonymous (2009) Pest watch: 1 April 2009 – 22 May 2009. Biosecurity 92(June): 33–35.

Antyukhova OV (2010) Beloakatzievaya mol-pestrianka (*Parectopa robiniella* Clemens) – opasnii vreditel *Robinia pseudoacacia* L. v Pridnestrovie [White acacia moth (*Parectopa robiniella* Clemens) – a dangerous pest of *Robinia pseudoacacia* L. in the Transnistria]. Izvestiya Sankt-Peterburgskoi Gosudarstvennoi Lesotekhnicheskoi Akademii 192: 4–11.

Bain J (2009) New insect on Robinia, *Obolodiplosis robiniae*. In: Farm Forestry New Zealand. https://www.nzffa.org.nz/farm-forestry-model/the-essentials/forest-health-pests-and-diseases/Pests/obolodiplosis-robiniae-robinia-gall-midge/new-insect-on-robinia/

Balk DL, Deichmann U, Yetman G, Pozzi F, Hay SI, Nelson A (2006) Determining global population distribution: Methods, applications and data. Advances in Parasitology 62: 119–156. https://doi.org/10.1016/S0065-308X(05)62004-0

Bartha D, Csiszár Á, Zsigmond V (2008) Black locust (*Robinia pseudoacacia* L.). In: Botta-Dukát Z, Balogh L (Eds) The most important invasive plants in Hungary. Institute of Ecology and Botany, Hungarian Academy of Sciences, Vácrátót, Hungary, 63–76.

Baugnée J-Y (2014) *Parectopa robiniella* (Lepidoptera: Gracillariidae), a leafminer of black locust *Robinia pseudoacacia*, new to the Belgian fauna. Phegea 42: 55–57. http://www.phegea.org/Phegea/2014/Phegea42-3_55-57.pdf

Bivand RS, Pebesema E, Gomez-Rubio V (2013) Applied spatial data analysis with R, 2nd edn. Springer, NY, [xviii +] 405 pp. https://doi.org/10.1007/978-1-4614-7618-4

Branco M, Nunes P, Roques A, Fernandes MR, Orazio C, Jactel H (2019) Urban trees facilitate the establishment of non-native forest insects. NeoBiota 52: 25–46. https://doi.org/10.3897/neobiota.52.36358

Buhl PN, Duso C (2008) *Platygaster robiniae* n. sp. (Hymenoptera: Platygastridae) Parasitoid of *Obolodiplosis robiniae* (Diptera: Cecidomyiidae) in Europe. Annals of the Entomological Society of America 101(2): 297–300. https://doi.org/10.1603/0013-8746(2008)101[297:PRNSHP]2.0.CO;2

Csóka G (2001) Recent invasions of five species of leafmining Lepidoptera in Hungary. In: Liebhold AM, McManus ML, Otvos IS, Fosbroke SLC (Eds) Proceedings „Integrated Management of Forest Defoliating Insects". USDA General Technical Reports NE-277: 31–36.

Csóka G, Pénzes Z, Hirka A, Mikó I, Matošević D, George M (2009) Parasitoid assemblages of two invading black locust leaf miners, *Phyllonorycter robiniella* and *Parectopa robiniella* in Hungary. Periodicum Biologorum 111(4): 405–411. https://hrcak.srce.hr/47878

Csóka G, Stone GN, Melika G (2017) Non-native gall-inducing insects on forest trees: a global review. Biological Invasions 19: 3161–3181. https://doi.org/10.1007/s10530-017-1466-5

Darling DC, Smith DR (1985) Description and life history of a new species of *Nematus* (Hymenoptera: Tenthredinidae) on *Robinia hispida* (Fabaceae) in New York. Proceedings of the

Entomological Society of Washington 87(1): 225–230. https://www.biodiversitylibrary.org/item/54866#page/233/mode/1up

Davis DR, De Prins J (2011) Systematics and biology of the new genus *Macrosaccus* with descriptions of two new species (Lepidoptera, Gracillariidae). ZooKeys 98: 29–82. https://doi.org/10.3897/zookeys.98.925

De Prins, J, De Prins W (2006–2020) Global taxonomic database of Gracillariidae (Lepidoptera). World Wide Web electronic publication. http://www.gracillariidae.net [date of accession 2021/05/03] https://doi.org/10.1163/9789004475397

de Rigo D, Caudullo G, Houston Durrant T, San-Miguel-Ayanz J (2016) The European Atlas of Forest Tree Species: modelling, data and information on forest tree species. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (Eds) European Atlas of Forest Tree Species. Publ. Off. EU, Luxembourg, 40–45. https://ies-ows.jrc.ec.europa.eu/efdac/download/Atlas/pdf/Modelling_data_and_information_on_forest_tree_species.pdf

Deschka G (1995) Schmetterlinge als Einwanderer. Stapfia 37: 77–128.

Dimić N, Dautbašić M, Magud B (2000) *Phyllonorycter robiniella* Clemens, a new leaf miner species in the entomofauna of Bosnia-Herzegovina. Works of the Faculty of Forestry, University of Sarajevo 1: 7–15.

Duso C, Skuhravá M (2002) First record of *Obolodiplosis robiniae* (Haldeman) (Diptera Cecidomyiidae) galling leaves of *Robinia pseudacacia* L. (Fabaceae) in Italy and Europe. Frustula Entomologica 25: 117–122.

Duso C, Boaria A, Surian L, Buhl PN (2011) Seasonal abundance of the Nearctic gall midge *Obolodiplosis robiniae* in Italy and the impact of its antagonist *Platygaster robiniae* on pest populations. Annals of the Entomological Society of America 104(2): 180–191. https://doi.org/10.1603/AN10030

ESRI (2016) ArcGIS j ArcMap 10.5 (10.5.1). Redlands, CA: Environmental Systems Research Institute. https://www.arcgis.com/features/index.html

Fagan WF, Lewis MA, Neubert MG, Van Den Driessche P (2002) Invasion theory and biological control. Ecology Letters 5(1): 148–157. https://doi.org/10.1046/j.1461-0248.2002.0_285.x

Fahrner S, Aukema BH (2018) Correlates of spread rates for introduced insects. Global Ecology and Biogeography 27: 734–743. https://doi.org/10.1111/geb.12737

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37: 4302–4315. https://doi.org/10.1002/joc.5086

Fodor E, Hâruța O (2009) Niche partition of two invasive insect species, *Parectopa robiniella* (Lepidoptera; Gracillariidae) and *Phyllonorycter robiniella* (Clem.) (Lepidoptera: Gracillariidae). Research Journal of Agricultural Science 41(2): 261–269. http://rjas.ro/download/paper_version.paper_file.8c94429aea2cc457.3336362e706466.pdf

Gilbert M, Liebhold A (2010) Comparing methods for measuring the rate of spread of invading populations. Ecography 33(5): 809–817. https://doi.org/10.1111/j.1600-0587.2009.06018.x

Gilbert M, Grégoire J-C, Freise JF, Heitland W (2004) Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria ohridella*. Journal of Animal Ecology 73: 459–468. https://doi.org/10.1111/j.0021-8790.2004.00820.x

Gippet JM, Liebhold AM, Fenn-Moltu G, Bertelsmeier C (2019) Human-mediated dispersal in insects. Current Opinion in Insect Science 35: 96–102. https://doi.org/10.1016/j.cois.2019.07.005

Guo Q, Fei S, Potter KM, Liebhold AM, Wen J (2019) Tree diversity regulates forest pest invasion. Proceedings of the National Academy of Sciences 116(15): 7382–7386. https://doi.org/10.1073/pnas.1821039116

Hambäck PA, Englund G (2005) Patch area, population density and the scaling of migration rates: the resource concentration hypothesis revisited. Ecology Letters 8(10): 1057–1065. https://doi.org/10.1111/j.1461-0248.2005.00811.x

Hargrove WW (1986) An annotated species list of insect herbivores commonly associated with black locust, *Robinia pseudoacacia*, in the Southern Appalachians. Entomological News 97(1): 36–40. https://www.biodiversitylibrary.org/page/2723423#page/290/mode/1up

Hastings A, Cuddington K, Davies KF, Dugaw CJ, Elmendorf S, Freestone A, Harrison S, Holland M, Lambrinos J, Malvadkar U, Melbourne BA (2005) The spatial spread of invasions: new developments in theory and evidence. Ecology Letters 8(1): 91–101. https://doi.org/10.1111/j.1461-0248.2004.00687.x

Hijmans RJ, Williams E, Vennes C (2019) geosphere: Spherical Trigonometry. https://cran.r-project.org/package=geosphere

Hudgins EJ, Liebhold AM, Leung B (2017) Predicting the spread of all invasive forest pests in the United States. Ecology Letters 20(4): 426–435. https://doi.org/10.1111/ele.12741

Huemer P (1993) Zur Arealexpansion zweier schädlicher Robinienminiermotten nach Österreich. Forstschutz aktuell 12/13: 11–12.

Huemer P, Deutsch H, Habeler H, Lichtenberger F (1992) Neue und bemerkenswerte Funde von Kleinschmetterlingen in Österreich. Berichte des Naturwissenschaftlich-medizinischen Vereins in Innsbruck 79: 199–202. https://www.zobodat.at/pdf/BERI_79_0199-0202.pdf

Huntley JC (1990) *Robinia pseudoacacia* L., Black Locust Leguminosae Legume family. In: Silvics of North America 2, 755–761. http://dendro.cnre.vt.edu/dendrology/USDAFSSilvics/40.pdf

Hurley BP, Garnas J, Wingfield MJ, Branco M, Richardson DM, Slippers B (2016) Increasing numbers and intercontinental spread of invasive insects on eucalypts. Biological Invasions 18: 921–933. https://doi.org/10.1007/s10530-016-1081-x

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17: 164–170. https://doi.org/10.1016/S0169-5347(02)02499-0

Kim, I-K, Park J-D, Shin S-C, Parek I-K (2011) Prolonged embryonic stage and synchronized life-history of *Platygaster robiniae* (Hymenoptera: Platygastridae), a parasitoid of *Obolodiplosis robiniae* (Diptera: Cecidomyiidae). Biological Control 57(1): 24–30. https://doi.org/10.1016/j.biocontrol.2010.12.007

Kodoi F, Lee H-S, Uechi N, Yukawa J (2003) Occurrence of *Obolodiplosis robiniae* (Diptera: Cecidomyiidae) in Japan and South Korea. Esakia 43: 35–41.

Liebhold AM, Yamanaka T, Roques A, Augustin S, Chown SL, Brockerhoff EG, Pyšek P (2018) Plant diversity drives global patterns of insect invasions. Scientific Reports 8(1): 1–5. https://doi.org/10.1038/s41598-018-30605-4

Liston AD (2011) New hostplant records for European sawflies (Hymenoptera, Tenthredinidae). Entomologist's Monthly Magazine 146: 189–193.

Lu C-K, Buhl PN, Duso C, Zhao C-M, Zhang J-S, Ji Z-X, Gao S-H, Yu J-Y, Wen X-L (2010) First discovery of *Platygaster robiniae* (Hymenoptera: Platygastridae) parasitizing the invasive *Obolodiplosis robiniae* (Diptera: Cecidomyiidae), a gall maker in China. Acta Entomologica Sinica 53(2): 233–237.

Maceljski M, Igrc J (1984) Bagremov miner (*Parectopa robiniella* Clemens (Lepidoptera, Gracillaridae) u Jugoslaviji. Zaštita bilja 35(4): 323–331.

Maceljski M, Mešić A (2001) *Phyllonorycter robiniella* Clemens a new insect pest in Croatia. Agriculturae Conspectus Scientificus 66(4): 225–230. https://hrcak.srce.hr/index.php?show=clanak_download&id_clanak_jezik=19256

Mally R, Ward S F, Trombik J, Buszko J, Medzihorský V, Liebhold A M (2021) European occurrence records of the *Robinia* herbivores *Parectopa robiniella*, *Macrosaccus robiniella* and *Obolodiplosis robiniella* compiled from literature records and personal observations. NeoBiota. https://doi.org/10.15468/qnrsen [accessed via GBIF.org on 2021-10-22]

Meier CM, Bonte D, Kaitala A, Ovaskainen O (2014) Invasion rate of deer ked depends on spatiotemporal variation in host density. Bulletin of Entomological Research 104(3): 314–322. https://doi.org/10.1017/S0007485314000042

Micieli De Biase L, Calambuca E (1979) L'*Appendiseta robiniae* (Gillette), nuova specie per l'italia su *Robinia pseudoacacia* L. Informatore Fitopatologico 11–12: 31–33.

Mihajlović L, Glavendekić MM, Jakovljević I, Marjanović S (2008) *Obolodiplosis robiniae* (Haldeman) (Diptera: Cecidomyiidae) – a new invasive insect pest on black locust in Serbia. Bulletin of the Faculty of Forestry 97: 197–208. https://doi.org/10.2298/GSF0897197M

Newman E (1837) Notes on Tenthredinina. The Entomological Magazine 4: 258–263. https://www.biodiversitylibrary.org/item/35924#page/278/mode/1up

Park J-D, Shin S-C, Kim C-S, Jeon M-J, Park I-K (2009) Biological characteristic of *Obolodiplosis robiniae* and control effects of some insecticides. Korean Journal of Applied Entomology 48(3): 327–333. https://doi.org/10.5656/KSAE.2009.48.3.327

Pebesma EJ, Bivand RS (2005) Classes and methods for spatial data in R. News, The Newsletter of the R Project 5: 9–13.

Prous M, Blank SM, Goulet H, Heibo E, Liston A, Malm T, Nyman T, Schmidt S, Smith DR, Vårdal H, Viitasaari M, Vikberg V, Taeger A (2014) The genera of Nematinae (Hymenoptera, Tenthredinidae). Journal of Hymenoptera Research 40: 1–69. https://doi.org/10.3897/JHR.40.7442

Rasplus J-Y, Villemant C, Rosa Paiva M, Delvare G, Roques A (2010) Hymenoptera. Chapter 12. In: Roques A, Kenis M, Lees D, Lopez-Vaamonde C, Rabitsch W, Rasplus J-Y, Roy D (Eds) Alien terrestrial arthropods of Europe. BioRisk 4: 669–776. https://doi.org/10.3897/biorisk.4.55

Rietschel G (1996) Zum Auftreten von *Phyllonorycter robiniella* (Clemens, 1859) (Lepidoptera, Gracillariidae), einer Miniermotte der Robinie, in Süddeutschland. Philippia 7(4): 315–318. https://www.zobodat.at/pdf/Philippia_7_0315-0318.pdf

Roques A, Auger-Rozenberg M-A, Blackburn TM, Garnas J, Pyšek P, Rabitsch W, Richardson DM, Wingfield MJ, Liebhold AM, Duncan RP (2016) Temporal and interspecific variation in rates of spread for insect species invading Europe during the last 200 years. Biological Invasions 18(4): 907–920. https://doi.org/10.1007/s10530-016-1080-y

Sautkin F, Evdoshenko S (2012) Sovremenoe rasprostranenie v usloviah Belarusii invazivnih vidov miniruiushih moley (Lepidoptera: Gracillariidae) – fillofagov-minerov beloi akatzii

(*Robinia pseudoacacia*) [Current distribution in Belarus of invasive species of miner moths (Lepidoptera: Gracillariidae) – phyllophagous miners of white acacia (*Robinia pseudoacacia*)]. Vestnik BGU 2(1): 103–104.

Šefrová H (2001) *Phyllonorycter robiniella* (Clemens, 1859) – egg, larva, bionomics and its spread in Europe (Lepidoptera, Gracillariidae). Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis 50(3): 7–12.

Šefrová H (2003) Invasions of Lithocolletinae species in Europe – causes, kinds, limits and ecological impact (Lepidoptera, Gracillariidae). Ekológia 22(2): 132–142.

Seljak G (1995) *Phyllonorycter robiniella* (Clemens), another new Lithocolletida of the Robinia in Slovenia. Gozdarski Vestnik 53: 78–82.

Serini GB (1990) Parassioidi di *Parectopa robiniella* Clemens e di *Phyllonorycter robiniellus* (Clemens) (Lepidoptera Gracillariidae). Bollettino di zoologia agraria e di bachicoltura 22(2): 139–149.

Shang X, Yao Y, Huai W, Zhao W (2015) Population genetic differentiation of the black locust gall midge *Obolodiplosis robiniae* (Haldeman) (Diptera: Cecidomyiidae): a North American pest invading Asia. Bulletin of Entomological Research 105: 736–742. https://doi.org/10.1017/S000748531500070X

Shigesada N, Kawasaki K, Takeda Y (1995) Modeling stratified diffusion in biological invasions. The American Naturalist 146(2): 229–251. https://doi.org/10.1086/285796

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biological invasions 1(1): 21–32. https://doi.org/10.1023/A:1010086329619

Sitzia T, Cierjacks A, de Rigo D, Caudullo G (2016) *Robinia pseudoacacia* in Europe distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (Eds) European Atlas of Forest Tree Species. Publ. Off. EU, Luxembourg, 166–167. https://ies-ows.jrc.ec.europa.eu/efdac/download/Atlas/pdf/Robinia_pseudoacacia.pdf

Skuhravá M, Skuhravý V, Csóka G (2007) Invasive spread of the gall midge *Obolodiplosis robiniae* in Europe. Cecidology 22: 84–90.

Stoch F (2003) Checklist of the species of the Italian fauna. https://www.faunaitalia.it/checklist/introduction.html

Stojanović A, Marković Č (2005) Parasitoid complex of *Phyllonorycter robiniella* (Clemens, 1859) (Lepidoptera, Gracillariidae) in Serbia. Journal of Pest Science 78: 109–114. https://doi.org/10.1007/s10340-004-0077-y

Therneau TM (2020) Survival Analysis [R package survival version 3.2-7]. https://cran.r-project.org/package=survival

Tokuda M, Uechi N, Yukawa J (2019) Invasive pest species of gall-inducing Cecidomyiidae (Diptera) in Japan. Formosan Entomology 38: 33–41. https://doi.org/10.6662/TESFE.2018017

Tomov RI (2003) *Phyllonorycter robiniella* (Clemens, 1859) (Lepidoptera, Gracillariidae), new pest on *Robinia pseudoacacia* L. in Bulgaria. Proceedings, scientific papers. The 50th anniversary of University of Forestry Sofia (2003): 105–107.

Tóth P, Váňová M, Lukáš J (2009) The distribution of *Obolodiplosis robiniae* on black locust in Slovakia. Journal of Pest Science 82: 61–66. https://doi.org/10.1007/s10340-008-0220-2

Uechi N, Yukawa J, Usuba S (2005) Recent distribution records of an alien gall midge, *Obolodiplosis robiniae* (Diptera: Cecidomyiidae) in Japan, and a brief description of its pu-

pal morphology. Kyushu Plant Protection Research 51: 89–93. https://doi.org/10.4241/kyubyochu.51.89

Vidano C, Marletto F (1972) *Parectopa robiniella* a new pest of *Robinia pseudacacia* in Europe. In: Proceedings: International Apicultural Congress, 23d, Moscow, 1971.

Vítková M, Müllerová J, Sádlo J, Pergl J, Pyšek P (2016) Black locust (*Robinia pseudoacacia*) beloved and despised: A story of an invasive tree in Central Europe. Forest Ecology and Management 384(2017): 287–302. https://doi.org/10.1016/j.foreco.2016.10.057

Ward SF, Fei S, Liebhold AM (2020) Temporal dynamics and drivers of landscape-level spread by emerald ash borer. Journal of Applied Ecology 57(6): 1020–1030. https://doi.org/10.1111/1365-2664.13613

Wein K (1930) Die erste Einführung nordamerikanischer Gehölze in Europa. Mitteilungen Deutsche Dendrologische Gesellschaft 42: 137–163.

Whitebread SE (1990) *Phyllonorycter robiniella* (Clemens, 1859) in Europe (Lepidoptera, Gracillariidae). Nota Lepidopterologica 12: 344–353. https://www.biodiversitylibrary.org/item/139985#page/360/mode/1up

Wojciechowicz-Żytko E, Jankowska B (2004) The occurrence and harmfulness of *Phyllonorycter robiniella* (Clem.), a new leafminer of *Robinia pseudoacacia* L. trees. Electronic Journal of Polish Agricultural Universities, Horticulture 7(1): [1–11]. http://www.ejpau.media.pl/articles/volume7/issue1/horticulture/art-06.pdf

Woo K-S, Choe HJ, Kim H-J (2003) A report on the occurrence of yellow locust midge *Obolodiplosis robiniae* (Haldeman, 1987) from Korea. Korean Journal of Applied Entomology 42(1): 77–79.

Yang Z-Q, Qiao X-R, Bu W-X, Yao Y-X, Xiao Y, Han Y-S (2006) First discovery of an important invasive insect pest, *Obolodiplosis robiniae* (Diptera: Cecidomyiidae) in China. Acta Entomologica Sinica 49: 1050–1053.

Supplementary material 1

Table S1. First record locations of *Parectopa robiniella*, *Macrosaccus robiniella* and *Obolodiplosis robiniae* from Europe.

Authors: Richard Mally

Data type: occurrences

Explanation note: An XLSX worksheet containing three tabs, one for each of the three investigated black locust herbivores *Parectopa robiniella*, *Macrosaccus robiniella* and *Obolodiplosis robiniae*, with the first locations (with country, administrative area, city and specific locality, where available), longitude, latitude, observation year and reference of the record.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.69.71949.suppl1

Supplementary material 2

Tables S2–S9

Authors: Richard Mally, Samuel F. Ward, Jiří Trombik, Jaroslaw Buszko, Vladimir Medzihorsky, Andrew M. Liebhold

Data type: docx. file

Explanation note: **Table S2.** Results of full Cox proportional hazards (CPH) models for all predictors with $p < 0.05$. **Table S3.** Results of full Cox proportional hazards (CPH) models with *Robinia* distribution removed as predictor, with $p < 0.05$. **Table S4.** Correlation matrix of predictors for best-fitting model for *Parectopa robiniella*. **Table S5.** Correlation matrix of predictors for best-fitting model for *Macrosaccus robiniella*. **Table S6.** Correlation matrix of predictors for best-fitting model for *Obolodiplosis robiniae*. **Table S7.** Akaike Information Criterion (AIC) values for *Parectopa robiniella*. **Table S8.** Akaike Information Criterion (AIC) values for *Macrosaccus robiniella*. **Table S9.** Akaike Information Criterion (AIC) values for *Obolodiplosis robiniae*.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.69.71949.suppl2